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Original Research Article

In vitro iron bioaccessibility and uptake from orange-fleshed sweet potato (*Ipomoea batatas* (L.) Lam.) clones grown in Peru

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ABSTRACT

Research to evaluate the potential of sweet potato to alleviate iron deficiency in affected human populations in developing countries is scarce. To partly fill this gap, we evaluated the bioaccessibility of iron in six sweet potato clones grown in two Peruvian environments, Satipo and San Ramon, following an *in vitro* gastro-intestinal digestion procedure. The bioaccessible iron content was clone-dependent and 1.7-fold higher in Satipo (5.15 μg/g of fresh weight (FW)) as compared to San Ramon (3.04 μg/g of FW). Aspects of iron bioavailability were then investigated using the Caco-2 cell model and ferritin synthesis as a marker, on two sweet potato clones after addition of an extrinsic source of iron to the digestion mixture.Results indicated that clone "CIP-194540.5" was presenting higher bioaccessible iron and lower phenolic contents and showed higher iron uptake as compared to clone "CIP-1055011.1" in both environments (91% *vs.* 24% in Satipo and 67% *vs.* 13% in San Ramon, respectively). These iron uptake values are higher than the ones previously reported for potato, which further stresses the use of sweet potato storage roots as part of a healthier diet in developing countries.

1. Introduction

Sweet potato (*Ipomoea batatas* (L.) Lam.) is one of the most important food crops worldwide, ranking seventh in terms of total crop production, with 104 million tons produced in 2014 (FAOSTAT data, 2017). Originating from South America, sweet potatoes are now grown and consumed in most tropical countries (Zhang et al., 2000). Orange-fleshed sweet potato has gained great interest in the past decade thanks to its remarkable nutritional value, especially its high concentration in pro vitamin A (Islam et al., 2016). Sweet potato roots provide energy through its high carbohydrate content and contain considerable amounts of vitamin C and pro-vitamins A particularly in orange-fleshed sweet potatoes, as well as of minerals such as potassium, calcium, magnesium, zinc and iron in a lower extent (Suarez et al., 2016). It is also considered as an important source of bioactive compounds such as phenolic compounds (Jung et al., 2011) and is also seen as functional food with its potential health-promoting capacities in the prevention or treatment of chronic diseases through its antioxidant, anti-inflammatory, immunomodulatory, anticancer/antitumour, antimicrobial and antiulcer activities (Ayeleso et al., 2016). Sweet potato presents a large genetic diversity reflected by a wide array of flesh and skin color, taste, shape, but also yielding potential, and stress susceptibility (Andrade et al., 2016). Initiatives aiming at substituting orange-fleshed sweet potatoes, rich in bioactive β-carotene, for white-fleshed sweet potatoes have been successful in alleviating vitamin A deficiency (van Jaarsveld et al., 2005; Low et al., 2007; Hotz et al., 2012a,b). The 2016 World Food Prize was awarded to 3 scientists from the International Potato Center (CIP) for their work on vitamin A-enriched sweet potato varieties with taste and agronomic characteristics that consumers and producers prefer, stressing the worldwide interest in sweet potato as part of a healthier diet in developing countries (Bouis and Saltzman, 2017).

Iron deficiency represents one of the most widespread forms of micronutrient malnutrition, especially in regions where meat consumption and therefore heme-iron intake is low (Lopez et al., 2016). In adults, iron deficiency anemia reduces physical performance, while its consequences during childhood and adolescence may be dramatic as physical and mental development is impaired (Falkingham et al., 2010). Non-heme iron bioavailability (the amount of ferric iron (Fe(III)) that can be absorbed and used for physiological function and/or

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storage) can be improved or impeded by the binding of iron to food compounds (Tako et al., 2014). It may be enhanced by simultaneous intake of vitamin C, citric acid, and animal proteins (Tako et al., 2015b), whereas phytates, calcium, and phenolic compounds may inhibit the absorption (Tako et al., 2014, 2015b; Andre et al., 2015; Hart et al., 2015; Tamilmani and Pandey, 2016).

Mineral biofortification of sweet potato could represent a promising strategy to alleviate iron deficiencies in affected human populations with high intake of sweet potato (Nestel et al., 2006). Biofortification has multiple advantages. First, it capitalizes on the regular daily intake of a consistent and large amount of food staples by low-income households. Second, after the one-time investment to develop seeds that fortify themselves, recurrent costs are low, and germplasm can be shared internationally. Third, once in place, nutritionally improved varieties will continue to be grown and consumed year after year, even if government attention and international funding for micronutrient issues fade. Fourth, biofortification provides a feasible means of reaching undernourished populations in relatively remote rural areas, delivering naturally fortified foods to people with limited access to commercially marketed fortified foods that are more readily available in urban areas (Nestel et al., 2006).

Large variations in iron concentrations of sweet potato roots have been reported in diverse sweet potato cultivars grown in Peru (Zum Felde et al., 2009), East Africa (Tumwegamire et al., 2011) and in Canary Islands (Luis et al., 2014; Suárez et al., 2016), indicating that breeding for increased iron content has good potential. Environmental growing conditions may, however, play determining roles in explaining iron, vitamin C, and phenolic acid concentrations (Andre et al., 2009; Chen et al., 2009).

The purpose of this work was to assess aspects of bioavailability of iron from diverse sweet potato cultivars grown in two different environments in Peru using the Caco-2 cells as a model of the human intestine. Ferritin level in cells is a sensitive marker of iron uptake and was used as a measurement of iron availability *in vitro* (Glahn et al., 1998). The bioaccessibility of iron, vitamin C and phenolic compounds, components that are known to interact with iron uptake, was first measured following an *in vitro* gastro-intestinal digestion procedure.

2. Materials and methods

2.1. Plant materials

Six orange-fleshed sweet potato clones from CIP's biofortified sweet potato population were used for this study. Samples were obtained from two field trials at CIP's experimental stations:

i) San Ramon (11°07′17′S 75°21′11″W, altitude 700 m): the trial was conducted from June 2013 to October 2013. During the growing period the average air temperatures varied between min. 10.3 °C and max. 17.0 °C, the daily cumulative precipitation was 9.4 mm, and the daily average incoming solar radiation was 193 W/m2 (NCEP, National Centers of Environmental Predictions, 2017).
ii) Satipo (11°15′08′S 74°38′19″W, altitude 628 m): the trial was carried out from July 2013 to December 2013. The average air temperatures ranged from 14.3 °C and max. 21.5 °C, the daily cumulative precipitation was 6.3 mm, and the daily average incoming solar radiation was 175 W/m2 (NCEP, National Centers of Environmental Predictions, 2017).

The pH of San Ramon and Satipo soil (5.22 *vs* 5.25), as well as the organic matter content (1.57 *vs* 1.30) were very similar. However, while the concentration of sand in the Satipo soil was lower than in San Ramon (52 *vs* 62%, respectively), the concentration of silt was higher in Satipo than in San Ramon (30% *vs* 22%, respectively).

Three to five representative roots from each orange-fleshed sweet potato clones were collected at harvest, washed and shipped to the Luxembourg Institute of Science and Technology (LIST), where they were stored in incubators at 10 °C prior to sampling and analysis. Roots were washed thoroughly with acidified water (pH = 3) in order to remove any soil residues and avoid mineral contamination of the samples. They were further rinsed with demineralized water. For cooking, demineralized water was added in stainless steel pots and brought to boiling on induction plates. Unpeeled roots were cooked for 20 to 40 min, depending on the size of the roots. Peeled and pureed orange-fleshed sweet potato roots were further submitted to the *in vitro* digestion protocol, while representative samples were frozen in liquid nitrogen, and kept at −80 °C until chemical analysis. The β-carotene concentration of these clones has been previously evaluated by HPLC at Quality and Nutrition laboratory using an HPLC method described in Burgos et al., 2014; and it ranges from 7.25 to 14.76 mg/100 g fresh weight (FW) in San Ramon and from 7.95 to 15.07 mg/100 g FW in Satipo (unpublished data).

2.2. In vitro digestion

The *in vitro* digestion protocol was performed as described in (Andre et al., 2015) on 10 g of boiled sweet potato flesh. The salivary, gastric, and intestinal digestion steps were performed in triplicate. Salivary digestion was first simulated by adding 5 mL of α-amylase in NaCl 0.9% (450 U/g of potato flesh) at pH 6.9 and shaking for 10 min at room temperature. For the gastric step, pepsin (6500 U/g of potato flesh) and 25 mL of NaCl 0.9% were added. The pH was decreased to 2 with HCl. The mixture was then shaken for 1 h at 37 °C. For the duodenal step, the pH was increased to 5.5 using $NaHCO_3$ 1 M. Bile extract (11 mg/g of sweet potato flesh) and pancreatin (1.8 mg/g of sweet potato flesh) were then added and the incubation volume was set to 50 mL. The digestion mixture (pH 7) was then further shaken for 2 h at 37 °C. The final digestion extract was centrifuged (5,000g for 20 min at 4 °C) and the supernatant was filtered (PVDF, 0.2 µm, PALL, Port Washington, NY, USA). Digests were then snap-frozen in liquid nitrogen and kept at −80 °C until further analysis. Procedure blanks were made using demineralized water and all digestive enzymes in the same conditions as with plant material. For iron uptake experiments, the frozen digests were quickly thawed by mixing in a water bath at 37 °C, appropriately diluted (5 or 10 times) and added onto the Caco-2 cells.

2.3. Determination of iron content

Boiled samples (about 1 g of fresh weight) were acid digested in 7 mL of nitric acid (HNO_3 for trace analysis min 67%) and 3 mL of H_2O_2 (30% *w/w*). For the mineralization of intestinal filtrates (3 mL), a mixture of 1.75 mL of HNO_3 and 0.75 mL of H_2O_2 was used. Acid mineralization was then performed in PFA tubes in a microwave oven (Anton Paar Multiwave Pro, Graz, Austria) by increasing temperature and pressure until 200 °C and 30 bar. At the end of the procedure, samples were diluted with demineralized water up to 25 mL for sweet potatoes and up to 10 mL for filtrates, and kept at 4 °C prior to analysis. Boiled and digested sweet potato samples, as well as procedure blanks were acid mineralized in triplicate and analyzed by inductively coupled plasma mass spectrometry (ICP-MS, Perkin Elmer Elan DRC-e, Waltham, MA, USA) (Lefèvre et al., 2012). Blanks for all samples and a certified reference material (Spinach, NCS ZC 73013, LGC standards, Molsheim, France) were included at each sample mineralization cycle (extraction yield was 89,36% ± 5,25%). For content determination, a six-point calibration curve (0.5–1250 µg/g) was used and quality controls were analyzed every 10th sample. The concentrations in aluminum and chrome were also determined for the detection of any potential soil contamination.

2.4. Vitamin C analysis

The extraction of vitamin C was performed in triplicate using an

aqueous solution containing 5% metaphosphoric acid and 1% dithiothreitol, as described in (Andre et al., 2007, 2015) on potato. Approximately 750 mg of boiled material was weighed in a 15 mL Falcon tube and 4 mL of an aqueous solution containing 5% metaphosphoric acid and 1% dithiothreitol were added. After shaking the samples for 1 h at 4 °C, the samples were centrifuged (5000*g*, 15 min, 4 °C). The supernatant was collected and the extraction was repeated. The pooled supernatants were filtered (0.2 µm) and analyzed by UPLC-DAD. The extraction was done in triplicate. For the analysis of digests, 0.5 mL of digest were mixed with 0.5 mL of an aqueous solution containing 10% metaphosphoric acid and 2% dithiothreitol, shaken for 30 s at 4 °C, centrifuged (5000*g*, 5 min, 4 °C), and filtered (0.2 µm) prior to analysis. The quantification was carried out using a Waters Acquity UPLC system (Milford, MA, USA) equipped with a photodiode array detector. An aliquot of 5 µL was injected onto an Acquity UPLC HSS T3 column (2.1 × 100 mm, 1.8 µm particle size, Waters, Milford, MA, USA) at 40 °C and a flow rate of 0.5 mL/min. The eluents were: 0.1% formic acid in water (A) and 0.1% formic acid in acetonitrile (B). The gradient was as follows: 0 min, 0% B; 1.5 min, 0% B; 2 min, 100% B; 5 min, 100% B; 5.5 min, 0% B; 7 min, 0% B. Ascorbic acid was detected at 243 nm according to its absorption maximum and quantified using a six-point calibration curve. Furthermore, a validation standard was injected after every 10th sample injection.

2.5. Phenolic compound analysis

The extraction of phenolic compound was conducted as described previously by (Andre et al., 2015). Briefly, approximately 750 mg of boiled material was weighed in a 15 mL Falcon tube and 10 mL of methanol/water/acetic acid (80:19.5:0.5, v/v/v). This mixture was homogenized using a vortex for 30 s and shaken for 2 h at room temperature. After centrifugation at 5000*g* for 15 min at 4 °C, the supernatant was collected and evaporated to dryness in a SpeedVac concentrator (Heto, Thermo Electron Corp., Waltham, MA, USA). Polyphenols were re-suspended in 1 mL of an aqueous solution containing 5% of methanol and filtered through a 0.2 µm PVDF syringe filter prior to UPLC-DAD injection. For the analysis of digests, 1 mL of filtered digest was kept in an amber HPLC vial prior to analysis. The quantification was carried out using the same equipment and column described for the vitamin C analysis. The injection volume was 10 µL, the column temperature 50 °C and the flow rate was 0.75 mL/min. The eluents were: 0.1% trifluoroacetic acid in water (A) and 0.1% trifluoroacetic acid in acetonitrile (B). The gradient was as follows: 0 min, 5% B; 9.27 min, 5% B; 13.53 min, 14% B; 22.60 min, 35% B; 23 min, 95% B; 25 min, 95% B; 26 min, 5% B. Phenolic compounds were detected at 320 nm and quantified using authentic standards and six-point calibration curves. The three di-caffeoylquinic acids were quantified as chlorogenic acid equivalents. For quantification, a six-point calibration curve was used. Furthermore, a validation standard was injected after every 10th injection.

2.6. Cell culture and ferritin measurement

The TC-7 Caco-2 subclone cells (ATCC no. HTB-37) were a generous gift from Monique Rousset (INSERM, Paris, France). Cells were maintained in FBS at 37 °C in an incubator with 10% CO_2/90% O_2 under constant humidity and grown in Dulbecco's modified Eagle medium + GlutaMAX (DMEM, Invitrogen, Halle, Belgium) with 10% Foetal Bovine Serum (FBS, Gibco, Halle, Belgium), 1% penicillin/streptomycin (Gibco, Hall, Belgium) and 1% non-essential amino acids (Sigma-Aldrich, St. Louis, MO). Cytotoxicity of the digestion mixtures was first determined using the resazurin/Alamar Blue assay (Thermo Fisher Scientific, Waltham, MA, USA). For that assay, cells were first seeded into 96-well plates at 1 × 104 cells per well and allowed to attach at 37 °C for 18 h. Cells were then exposed to digests for 24 h. Culture medium was then removed and 100 µL of cell culture medium containing 500 µM of resazurin were added to each well. After two to three hours, the formation of resorufin by cellular metabolic activity was recorded using a microplate fluorometer (excitation wavelength 530 nm, emission at 590 nm, 37 °C). A negative control with no cells was used for background subtraction. The percentage of cell viability was calculated using the non-treated cells as positive control (100% cell viability). At the concentration of 20% of digest and below, the cell viability was above 70% for all sweet potato genotypes.

Cells, used at passage (number of divisions cells have had in culture) between 52 and 85, were seeded (50,000 cells/cm^2) into 6 well plates (VWR, Radnor, PA, USA). After seeding, cells were maintained in DMEM supplemented with 2% FBS, which was changed every couple of days. Cells were used for experiments 14 days after seeding. The integrity of the cell monolayer was verified by optical microscopy. Forty-eight hours prior to the experiment, the growth medium was removed from culture wells, the cell layer was washed with phosphate buffered saline (PBS, Gibco, Halle, Belgium), and the growth medium was replaced with a supplemented minimum essential media (MEM) at pH 7.0 as described in (Glahn et al., 1998). Caco-2 cells were directly treated with or without 4 µM of $FeCl_3$ and 1 mM of ascorbic acid to induce ferritin synthesis, as well as with or without solutions containing 10 or 20% of intestinal filtrate diluted in MEM (v/v). Incubation was done for 24 h. Total protein content was of 509 µg on average per well. After lysing cells, ferritin levels were determined using the human ferritin enzyme-linked immunosorbent assay (ELISA) kit provided by Biovendor (Brno, Czech Republic). Results were normalized by total protein concentration measured by spectrophotometry using a Bradford kit (Biorad, Hercules, CA, USA) and bovine serum albumin (BSA) as a standard. Data are expressed as a percentage of the ferritin of the reference control (4 µM of $FeCl_3$ + 1 mM of ascorbic acid).

2.7. Statistical analyses

Pearson and Spearman Rank correlation coefficients were determined on (log-transformed) data to evaluate relationships between variables. Two-way ANOVA and Tukey tests were carried out to determine the significant influences of the clones and of the environment. Normality tests and equality of variance were first performed. For these purposes, the statistical software SigmaPlot version 12.5 (Systat Software Inc., San Jose, CA, USA) was used. Principal component analysis (PCA) was performed on standardized data to evaluate the phytochemical profile of the different clones across the environments using the PAST 3.x software (Hammer et al., 2001).

3. Results and discussion

3.1. Concentration and bioaccessibility of iron

The average iron concentration in boiled sweet potato roots was 8.39 µg/g FW in Satipo and 6.33 µg/g FW in San Ramon (Table 1). No apparent soil contamination was present as the concentrations of aluminium and chrome were below 0.5 and 0.01 µg/g, respectively. Differences in soil structure between Satipo and San Ramon (Satipo has lower sand and higher silt concentration than San Ramon) could be contributing to the differences in the mean iron concentration. Although the average iron value was significantly higher in Satipo ($p < 0.001$) (Table 2), there was no significant consistency in the ranking of the cultivars between the different growing environments in terms of boiled sweet potato root iron content (Spearman Rank Correlation Coefficient > 0.05). It appears that there is a strong influence of clone and environment as well as of their interaction on iron accumulation in sweet potato roots, as it is revealed by the two-way analysis of variance (Table 2).

The mean iron concentration in the biofortified clone CIP-189153.8 as grown in Satipo reaches 10.41 µg/g FW. This value is higher than the mean iron concentration of non-biofortified varieties from Eastern

Table 1
Mean total iron content in boiled sweet potato roots of six clones grown in two environments in Peru (Satipo and San Ramon). The mean *in vitro* iron bioaccessibility as well as the percentage of iron released during the in vitro digestion is also presented for each clone. Data are expressed in μg/g of fresh weight (FW) and represent mean ± SD (n = 3). * and ** indicate a significant influence of the environment for a particular clone (Tukey test, $p < 0.05$ and $p < 0.01$, respectively).

Clone *Location*	% of Dry Weight	Total iron in boiled roots (μg/g FW)	Total bioaccessible iron (μg/g FW)	% Release
CIP-194540.5				
Satipo	34.33	8.59 ± 0.78	5.77 ± 0.02	67.18
San Ramon	32.53	7.02* ± 0.05	4.09** ± 0.23	58.19
CIP-190094.91				
Satipo	26.87	8.65 ± 1.19	5.86 ± 0.24	67.74
San Ramon	26.04	6.01* ± 0.59	3.86** ± 0.66	64.31
CIP-189165.9				
Satipo	26.00	7.78 ± 0.48	4.40 ± 0.34	56.56
San Ramon	25.17	6.20* ± 0.53	2.24** ± 0.05	36.04
CIP-189153.8				
Satipo	22.52	10.41 ± 0.71	5.51 ± 0.27	52.97
San Ramon	26.75	6.11** ± 0.45	1.52** ± 0.25	24.90
CIP-105523.1				
Satipo	30.20	9.67 ± 0.91	5.85 ± 0.51	60.51
San Ramon	29.23	7.63* ± 0.05	3.79** ± 0.33	49.61
CIP-105511.1				
Satipo	15.73	5.26 ± 0.20	3.50 ± 0.35	66.52
San Ramon	23.35	4.98 ± 0.24	2.77* ± 0.34	55.63
Overall Mean				
Satipo		8.39	5.15	61.91
San Ramon		6.33	3.04	48.11

Africa (6.48 μg/g FW, Tumwegamire et al., 2011). Hence, this biofortified clone could provide a feasible mean of reaching undernourished populations in relatively remote rural areas of Eastern Africa, delivering naturally fortified foods to people with limited access to commercially marketed fortified foods that are more readily available in urban areas. Biofortified varieties may have important spin-off effects for increasing farm productivity in developing countries in an environmentally beneficial way (Nestel et al., 2006). However, as suggested above, the environment may have a strong influence, and therefore the iron concentration of this clone should be evaluated under Eastern African conditions to better estimate the potential of this clone.

The percentage of iron bioaccessibility of the six clones ranged from 53 to 67.7% in Satipo and from 24.9% to 64.3% in San Ramon and from with an average value of 61.9% for the ones grown in Satipo and of 46.5% for clones grown in San Ramon. These values are above the percentage iron bioaccessibility reported for most cereals and legumes (Luo et al., 2014), but slightly lower than the one found for potato tubers (70%) (Andre et al., 2015). It is likely that some root components such as the composition and configuration of the carbohydrate polymers play a role on the extent of iron release, as it has been shown in infant formula supplemented with various types of dietary fibers (Bosscher et al., 2003). As for potato, starch is the most important carbohydrate component in the sweet potato storage root (beside large concentrations of different sugars) (Tumwegamire et al., 2011). However, as compared to the starch of potato tubers, sweet potato starch exhibits lower granular size and lower pasting viscosity (Kitahara et al., 2017), which could partly explain differences in terms of mineral availability.

The average bioaccessible iron content of the six clones was significantly higher in Satipo (5.15 μg/g FW) as compared to San Ramon (3.04 μg/g FW), partly due to significantly higher boiled root iron content and increased release from the sweet potato matrix (Table 1 and 2). To our knowledge, this is the first report on the bioaccessibility of iron from sweet potato storage roots.

3.2. Bioaccessibility of vitamin C and phenolic compounds

The overall mean total ascorbate contents in boiled sweet potato roots of the six clones were 170.5 and 273.4 μg/g FW in Satipo and San Ramon (Table 3), respectively. These values are in general agreement with the vitamin C concentration reported in the USDA database (USDA, 2015, food code 11510) with a significant influence of clone and environmental factors (Two-way analysis of variance, $p < 0.001$, Table 4). A significant interaction between clone and environment was also clear, indicating that the vitamin C content of the different clones did not vary to the same extent across environments. The mean bioaccessible vitamin C concentrations were 71.3 and 89.8 μg/g FW from Satipo and San Ramon, respectively, with a stronger effect of the clone ($p < 0.001$) over the environment ($p = 0.002$). The percentage of vitamin C bioaccessibility of the six clones ranged from 26% to 51% in San Ramon and from 34% to 51% in Satipo, with no significant influence of the environment ($p = 0.061$), suggesting that components of the sweet potato matrix interfering with vitamin C bioaccessibility (*e.g.* proteins, antioxidants, or minerals (Rodriguez-Roque et al., 2015)) are not directly influenced by the growing conditions.

The phenolic profile of sweet potato roots was evaluated by UPLC-DAD. The chromatogram at 280 nm and 320 nm was dominated by hydroxycinnamic acids, as previously described (Truong et al., 2007; Lebot et al., 2016). In the profile, three isomers of caffeoyl-quinic acids (CQA), namely neochlorogenic (5-CQA), cryptochlorogenic (4-CQA) and chlorogenic acid (3-CQA) acids, as well as three di-caffeoyl quinic acids (4,5-di-CQA, 3,5-di-CQA, and 3,4-di-CQA), were detected and identified by comparison with authentic standards and their UV spectra and retention time data as compared to published data (Truong et al., 2007; Lebot et al., 2016) (Fig. 1). Di-CQAs were quantified as 5-CQA equivalents. The overall mean total phenolic contents in boiled sweet potato roots were 861 and 758 μg/g FW in Satipo and San Ramon (Table 3), respectively, which is in good agreement with published data (Truong et al., 2007; Grace et al., 2014). A significant effect of the clone could be stressed, whereas the environment did not significantly influence the phenolic concentrations (Table 5). The percentage bioaccessibility of total phenolic acids was not influenced by the environments either, with overall mean values of 99% and 104% for sweet potato roots grown in Satipo and San Ramon, respectively. These

Table 2
Results of the two-way analysis of variance performed for total iron contents before (Boiled) and after *in vitro* digestion (Bioaccessible), and percentage of bioaccessibility on the roots of 6 sweet potato clones grown in two environments (Satipo and San Ramon,Peru).

Source of variation	d.f.	Total Iron − Boiled		Total Iron − Bioaccessible		Total Iron − Percentage of bioaccessibility	
		F-value	*p-value*	*F-value*	*p-value*	*F-value*	*p-value*
Clone		19.323	< 0.001	14.224	< 0.001	16.255	< 0.001
Environment		212.06	< 0.001	492.678	< 0.001	41.784	< 0.001
Clone − Environment		19.29	< 0.001	25.939	< 0.001	2.874	0.036
Residual	24						

Table 3
Mean total ascorbate and phenolic concentrations of boiled roots and of their *in vitro* bioaccessible fractions in 6 sweet potato clones grown in two environments, Satipo (SA) and San Ramon (SR). Data are expressed in µg per g of fresh weight (FW) (n = 3). Letters (A to H) correspond to the peaks identified in Fig. 1.

Clones	CIP-194540.5				CIP-190094.91				CIP-189165.9				CIP-189153.8				CIP-105523.1				CIP-105511.1			
	Boiled		Bio-accessible		Boiled		Bio-accessible		Boiled		Bio-accessible		Boiled		Bio-accessible		Boiled		Bio-accessible		Boiled		Bio-accessible	
	SA	SR	SA	SR	SA	SR	SA	SR	SA	SR	SA	SR	SA	SR	SA	SR	SA	SR	SA	SR	SA	SR	SA	SR
Compounds																								
Total Ascorbate	218	257	111	102	73.3	162	35.7	54.7	208.3	248.7	82.9	96.2	232	258	93.0	83.4	157	400	52.8	104	133	194	53.0	99.0
3-caffeoylquinic acid (C)	159	259	172	308	286	165	325	243	469.6	470.2	54	447	151	119	166	157	216	114	263	142	132	280	155	355
5-caffeoylquinic acid (A)	37.8	31.9	9.3	25.4	51.6	16.1	47.6	20.3	88.1	45.6	27.6	2.5	46.8	16.8	16.7	1.3	28.1	14.6	103	0.9	37.3	23.6	63.6	1.2
4-caffeoylquinic acid (D)	74.5	110	114	102	40.6	76.8	256	111	38.7	188.8	51.5	78.8	78.1	63.1	36.5	16.6	97.2	53.8	68.5	27.5	106	124	29.1	110
Caffeic Acid (B)	3.4	5.2	1.6	1.1	4.0	2.2	3.8	0.8	5.3	14.8	3.4	1.7	9.5	8.4	2.5	0.6	8.8	3.1	4.1	1.1	5.5	20.1	3.2	2.0
Ferulic Acid (E)	0.8	0.7	0.5	0.4	0.6	0.4	nd[a]	0.3	0.5	0.6	nd	0.6	0.7	0.6	nd	0.5	0.5	0.8	nd	0.4	0.7	0.5	0.5	0.7
4,5-di-caffeoylquinic acid (F)	50.5	45.9	62.1	47.2	70.9	46.6	127	55.5	160	169	160	152.0	193	145	128	145	148	32.4	116	38.0	122	182	34.5	198
3,5-di-caffeoylquinic acid (G)	81.7	73.8	99.5	73.2	173	78.4	189	97.7	225	295	247	258	251	234	198	253	229	55	194	66.6	206	303	116	333
3,4-di-caffeoylquinic acid (H)	51.8	42.9	75.9	50.1	161	37.8	180	44.3	202	172	216	1503	254	143	164	136	230	30.4	153	33.9	177	227	92.0	214
Total Phenolics	460	569	535	608	787	423	1128	572	1189	1356	1255	1091	984	732	710	710	957	304	901	310	786	1160	495	1214

[a] nd = not detected. Limit of detection (LOD) for ferulic acid was 0.1 µg/g FW.

percentages of bioaccessibility are generally higher than the ones we obtained for potato tubers (Andre et al., 2015) using the same digestion protocol, pointing out the likelihood of differences between the matrix of potato tubers and sweet potato roots. The bioaccessible phenolic concentrations for the six clones ranged from 495 (for the clone CIP-105511.15) to 1255 µg/g FW (for the clone CIP-189165.9) and from 310 (for the clone CIP-105523.1) to 1214 µg/g FW (for the clone CIP-105511.1) when grown in Satipo and San Ramon, respectively. These high bioaccessible values for phenolic compounds may however not reflect their bioavailability as it is well known that these molecules are not well absorbed by intestinal cells in their native forms and that most of them are biotransformed by the gut microbiota (Mena and Llorach, 2017).

A principal component analysis (PCA) was performed in order to highlight the differences between the clones grown in the two distinct environments (Fig. 2). PCA was carried out on the 6 clones grown in Satipo and San Ramon and included 10 variables consisting of the measurements reported in Table 1 and 3. The first two principal components (PC) accounted for 66.1% of the total variance. The influence of the environment on iron, vitamin C and 3-CQA content appears along PC2, whereas large variability between the clones can be observed in terms of phenolic composition according to PC1. Clones grown in Satipo, except for the clone CIP-194540.5, were positively correlated with PC2 and were characterized by higher iron and 3-CQA root amounts. The clones CIP-190094.91, CIP-105523.1, and CIP-194540.5 were negatively correlated with PC1, suggesting lower root amounts of 5-CQA and di-caffeoylquinic acids. On the basis of this study, two contrasting clones were chosen to study aspects of iron bioavailability from sweet potato roots, *i.e.* CIP-105511.1 and CIP-194540.5.

3.3. Aspects of in vitro iron bioavailability

The Caco-2 intestinal cell culture model was used to evaluate iron uptake from sweet potato roots coming from two clones (CIP-105511.1 and CIP-194540.5) grown in Satipo and San Ramon. The caco-2 cells are derived from a human colorectal adenocarcinoma and may differentiate and polarised to form intestinal cell monolayers. This model has been shown to be effective in comparing iron uptake from diverse genotypes of bean, rice, maize, and potato (Glahn et al., 2002; Ariza-Nieto et al., 2007; Beiseigel et al., 2007; Tako et al., 2014; Tako et al., 2015a,b). Using this model, ferritin concentrations in cells are used as a marker of iron uptake, which enable measurement of iron bioavailability *in vitro* (Glahn et al., 1998).

The toxicity of the sweet potato digests on this model has first been evaluated and showed no significant cell death at a concentration of 20% and below. Whereas the basal ferritin level was 3 ng/mg of protein (control exposed to a blank digest), an increase of ferritin expression up to 174 ng/mg of protein was observed when exposed to 4 µM $FeCl_3$ (+1 mM ascorbic acid). The absorption of intrinsic iron from sweet potato roots was however not detected using our *in vitro* intestinal cell model, as previously reported in other studies on high phenolic-containing food (Ariza-Nieto et al., 2007; Tako et al., 2014; Andre et al., 2015). Although this model has been shown to be very useful at comparing different matrices or plant varieties (Glahn et al., 2002; Tako et al., 2014), it appears to have sensitivity issues and an *in vivo* validation would definitely be needed to confirm our data. Indeed, we cannot exclude that the bioaccessible iron from sweet potato is actually absorbed in humans. In rats, it has been shown that chlorogenic acid complexes iron and inhibits to some extent intestinal iron absorption (Gutnisky et al., 1992).

The influence on the uptake of extrinsic iron was investigated in order to better understand how sweet potato components interact with iron and its absorption (Fig. 3). Accordingly, when adding 4 µM of $FeCl_3$ and 1 mM of ascorbic acid together with 20% of sweet potato digests, ferritin synthesis was induced in a clone- and environment-dependent manner (Fig. 3A). The clone "CIP-105551.1" showed iron

Table 4
Results of the two-way analysis of variance performed for total ascorbate contents before (Boiled) and after *in vitro* digestion (Bioaccessible), and percentage of bioaccessibility on the roots of 6 sweet potato clones grown in two environments, Satipo and San Ramon, Peru.

Source of variation	d.f.	Total Ascorbate − Boiled		Total Ascorbate − Bioaccessible		Total Ascorbate − Percentage of bioaccessibility	
		F-value	*p-value*	*F-value*	*p-value*	*F-value*	*p-value*
Clone		31.734	< 0.001	19.701	< 0.001	3.760	0.012
Environment		69.32	< 0.001	11.958	0.002	3.85	0.061
Clone − Environment		21.675	< 0.001	7.438	< 0.001	2.321	0.075
Residual	24						

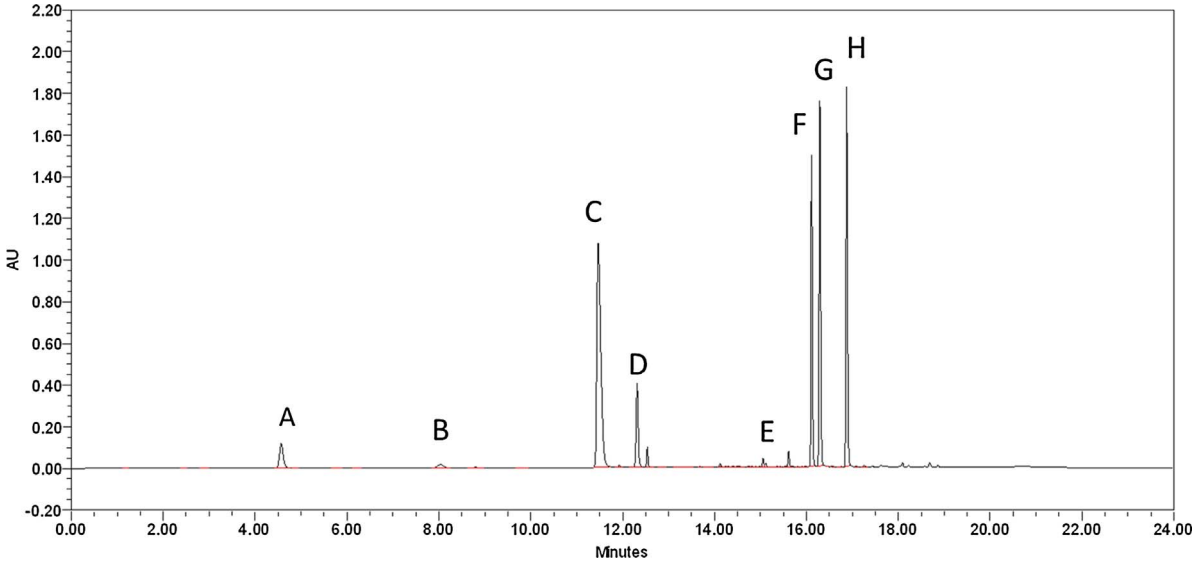

Fig. 1. Phenolic UPLC-DAD profile of boiled sweet potato root (CIP-189153.8, grown in Satipo) recorded at 320 nm. Peak assigments: 5-caffeoylquinic acid (A), caffeic Acid (B), 3-caffeoylquinic acid (C), 4-caffeoylquinic acid (D), ferulic Acid (E), 4,5-di-caffeoylquinic acid (F), 3,5-di-caffeoylquinic acid (G), 3,4-di-caffeoylquinic acid (H).

Table 5
Results of the two-way analysis of variance performed for total phenolic contents before (Boiled) and after *in vitro* digestion (Bioaccessible), and percentage of bioaccessibility on the roots of 6 sweet potato clones grown in two environments, Satipo and San Ramon, Peru.

Source of variation	d.f.	Total Phenolics − Boiled		Total Phenolics − Bioaccessible		Total Phenolics − Percentage of bioaccessibility	
		F-value	*p-value*	*F-value*	*p-value*	*F-value*	*p-value*
Clone		29.211	< 0.001	24.953	< 0.001	4.345	0.006
Environment		3.519	0.073	4.202	0.051	0.00253	0.96
Clone − Environment		3.044	0.029	13.29	< 0.001	1.982	0.118
Residual	24						

uptake values (24% in Satipo *vs*. 13% in San Ramon) consistently lower than the ones of the clone “CIP-194540.5” (91% in Satipo *vs*. 67% in San Ramon). This result could partly be explained by the lower concentrations of phenolic compounds in “CIP-194540.5” as compared to “CIP-105551.1”. For both clones, higher ferritin values were obtained when grown in Satipo, which could partly be due to higher bioaccessible iron values and lower phenolic content (Fig. 2). Ferritin synthesis was further increased when the sweet potato digests were diluted twice (representing 10% of the total media above the cells) (Fig. 3B), with even a promoting effect of the digest coming from the clone “CIP-194540.5” grown in Satipo (169%). There are several hypotheses that could explain this observation: i) the presence of unknown sweet potato components favours the passage of extrinsic iron from the apical compartment into the cells, ii) the presence of extrinsic iron together with ascorbic acid may react and inhibit the action of some sweet potato components that were preventing intrinsic iron to absorbed. We also cannot exclude that higher bioaccessible (intrinsic) iron content and/or the trend to lower phenolic content does not play a role in explaining the higher ferritin percentage observed for the clones grown in Satipo as compared to San Ramon. When compared to potato tubers analyzed with a similar methodology and compared to the same reference control (4 μM of $FeCl_3$ + 1 mM of ascorbic acid) (Andre et al., 2015), the iron uptake percentages of sweet potato roots appear to be two- to thirteen-fold higher. Whereas both potato tubers and sweet potato roots are considered as rich sources of starch and dietary fibers, their differences in terms of nutritional composition (Woolfe and Poats, 1987; USDA, 2015) could partly explain this result: sweet potato roots contain higher amount of total carbohydrates (in addition to starch structural differences, see comment above), more fat, more dietary fibers, more carotenoids, and lower protein content, as compared to potato tubers.

4. Conclusions

The bioaccessible iron contents from sweet potato roots were both clone- and environment-dependent, with on average two-fold higher values observed in Satipo as compared to San Ramon. The intestinal absorption of intrinsic iron from sweet potato roots could not be detected using our *in vitro* Caco-2 cell model, which has previously been

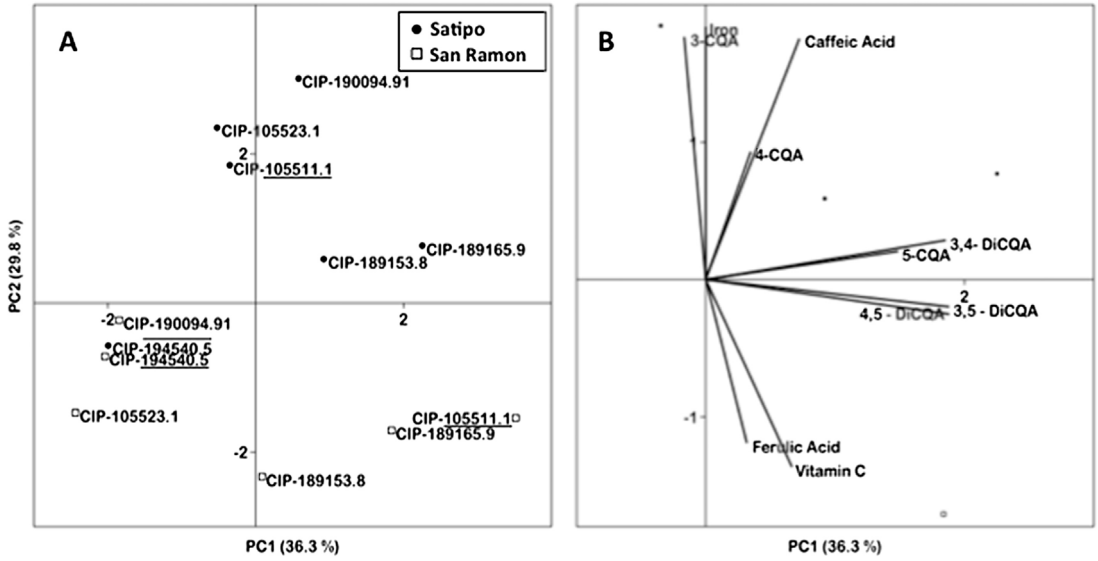

Fig. 2. Principal component analysis (PCA) resulting from the *in vitro* digestion of 6 sweet potato clones grown in two environments. (A) Score plots of the 6 sweet potato clones grown in two environments: Satipo (black circle) and San Ramon (white square). (B) Loading plot showing the relationships between the 10 variables.

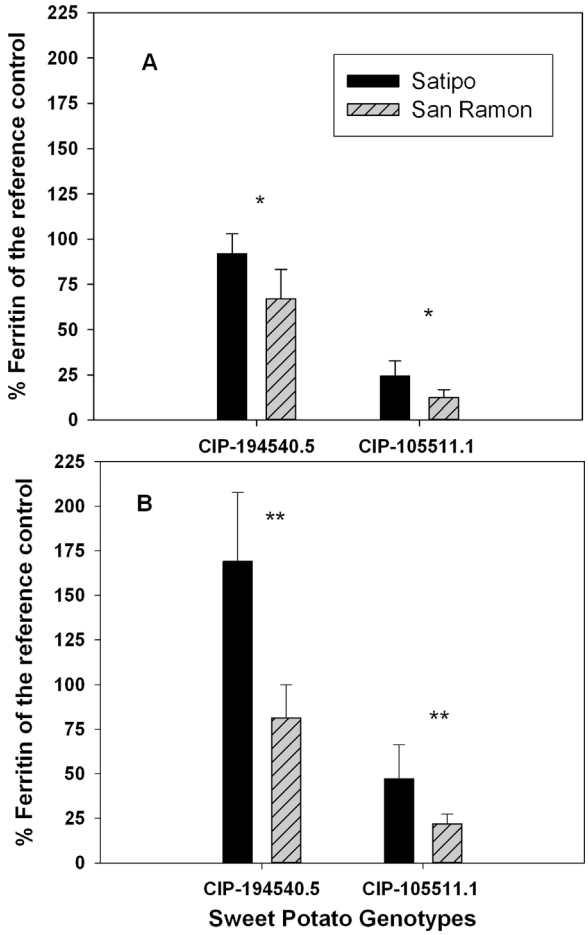

Fig. 3. Extrinsic iron uptake values in presence of digests from 2 sweet potato clones grown in two environments as measured by ferritin expression in Caco-2 cells. Ferritin expression was evaluated by an ELISA assay and normalized by total protein concentrations. Caco-2 cells were exposed to 20% (A) or 10% (B) of sweet potato digest supplemented with iron (4 μM of $FeCl_3$) and ascorbate (1 mM). The data are presented as percentage of the positive control (exposure to digest blank containing 4 μM of FeCl3 and 1 mM of vitamin C). Values are means ± SEM (n = 9, resulting from three independent experiments). *Significant difference at the $p < 0.05$ level; **Significant difference at the $p < 0.01$ level.

described for other foods containing high concentrations of phenolic compounds such as potato and bean. With the addition of an extrinsic source of iron to the digestion mixture, our model could however allow us to compare the behavior of two different cultivars grown in two environments. Importantly, we showed that the clone “CIP-194540.5” presented reliably higher ferritin values than clone “CIP-105551.1” in both environments at two different concentrations. We hypothesized that this difference could be due to higher bioaccessible iron values, lower phenolic content, the presence of extrinsic iron together with ascorbic acid inhibiting the action of some “CIP-194540.5” root components that were preventing intrinsic iron to be absorbed, or a combination of these effects. Such results may help plant breeders working on increasing the bioavailable content of iron and/or reducing the amount and type of iron uptake inhibitors in sweet potato. Controlled trials on human volunteers will however be needed to obtain a precise percentage of iron absorption from sweet potato roots.

Conflict of interest

The authors declare no conflict of interest.

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